Quantitative Relationships Between Gill Number, Respiratory Surface, and Cavity Shape in Chitons

BY

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(6 Text figures)

INTRODUCTION

Chitons have a number of characteristics which suggest that they are a very primitive group of mollusks: an ovoid shape, a broad, flat foot, shells of only two layers – the tegmentum and the articulamentum – , a microphagous, herbivorous mode of feeding, a non-ganglionated nervous system, and a trochophore larva which metamorphoses directly into the adult form. Yet, with all of these primitive characteristics they are not termed an "ancestral mollusk" type. That is largely because of the many gills found in the grooves along the sides of the foot.

Yonge (1939, 1947) describes an "ancestral mollusk" with a posterior mantle cavity with only 2 gills. He believes that the chitons evolved from this ancestor due to a flattening of the animal with an extension of the pallial cavity in grooves alongside of the body. The gills were seemingly forced into multiplying in number and shortening so as to fit into the grooves.

Until recently Yonge's hypothesis was not challenged. With the discovery of *Neopilina galathea* Lemche, 1957, a doubt as to the complete validity of Yonge's hypothesis was raised. *Neopilina* was obviously a very primitive mollusk with its ovoid shell, flat foot, and radula. But the most astonishing fact was that it had a series of gills along the side of the foot. To Lemche (1957) this was enough to prove that multiplicity of gills was the primitive condition of the molluscan pallial cavity and also enhanced the idea that mollusks had a segmented ancestor. So, from Lemche's hypothesis it could be concluded that the gills in chitons are arrayed like the primitive condition and that the number of gills in other groups of mollusks is a reduction.

Only Hunter & Brown (1965) have tried studying the gills in chitons in an attempt to show with data just which theory might be reasonable. Hunter & Brown studied only the relationship between the weight-length and the number of gills. Their results showed what they considered too great an asymmetry between the number of gills on each side of animals of equal weight-length for there to be any basis for the idea that chitons are related to a segmented ancestor. And, therefore, the condition of the gills was not even possibly like the primitive state. In other words, they decided that the gills were a secondary replication of structures of the 'ancestral mollusk' as Yonge had hypothesized it.

Hunter & Brown may have been correct in concluding that the asymmetry in gill numbers may show a lack of segmentation. But that does not necessarily mean that a multiplicity of gills was not a primitive condition of the mollusks. There are 3 groups which are very primitive mollusks and do have numerous gills – *Neopilina, Nautilus,* and the chitons. So, why could not the primitive condition have been a "mantle cavity as a groove bounded by the mantle edge and surrounding the head-foot rather than a posterior cavity"? (Fretter & Graham, 1962).

Hunter & Brown used only 2 species, *Chaetopleura apiculata* (Say, 1834) and *Lepidochitona cinereus* (Linnaeus, 1767). And they only counted the number of gills. I have sought to further clarify that picture of the chiton gill cavity by making additional measurements.

MATERIALS AND METHODS

Various measurements of a chiton's gill cavity assist in portraying the gills in relation to the whole animal: (1) the length of the animal along the foot; (2) lengths of the gill series on both sides; and (3) the length of the most posterior gill itself. Also, I counted the number of gills on both sides of the animal. And by likening the effective gill surface (that which water must pass through during respiration) to a triangle I could compute that surface area by using the length of the last gill and the length of the gill series in the formula: $\frac{1}{2}bh =$ area of a triangle.

These various measurements can be used for a description of the gill cavities of a group of chitons with a wide range of types, sizes, and shapes. I used chitons from 2 suborders and 4 families of different adult lengths and shapes, and of a range of sizes within each species. The species I used are further described below:

Acanthochitonina

Acanthochitonidae

1. *Acanthochitona exquisita* Pilsbry, 1893, is a small (1.1 to 3.3 cm) oblong chiton.

Lepidopleurina

Ischnochitonidae

1. *Stenoplax (Stenoradsia) magdalenensis* (Hinds, 1844) is a long (2.1 to 9.0 cm), rather narrow chiton.
2. *Tonicella lineata* (Wood, 1815) is a small chiton (1.8 to 4.4 cm). Its general shape is a gently rounded oblong.

Mopalidae

1. *Mopalia muscosa* (Gould, 1846) is a large (1.1 to 8.1 cm) oval chiton.
2. *Placiphorella velata* Dall, 1879 is a small (0.9 to 2.5 cm) broad, oval, flattened chiton.

Chitonidae

1. *Chiton sulcatus* Wood, 1815 is a large (0.5 to 7.5 cm) chiton which is fairly broad and oval.

All of the specimens were preserved in the collection at the Department of Invertebrate Zoology, California Academy of Sciences, San Francisco. So, I tried to look at a range in sizes of each species of chiton that had come from one collecting area. In that way I could possibly be working on a growth series of a species. Therefore, I chose the following lots:
100 *Acanthochitona exquisita* from Puerto Refugio, Angel de la Guarda Island, Gulf of California; 25 *Stenoplax magdalenensis* from Punta Abreojos, Baja California; 92 *Tonicella lineata* from False Bay, San Juan Island, Puget Sound, Washington; 20 *Placiphorella velata* from Cedros Island, Mexico; 40 *Chiton sulcatus* from near and in Academy Bay, Santa Cruz Island, Galápagos Islands.

Mopalia muscosa was the exception. The Academy did not have a large number of animals from any one place. Therefore I took groups which had been collected along the range of this species. Thus, 17 *M. muscosa* were from False Bay, Washington; 8 from near San Simeon, California; and 10 from one mile north of Camalu Arroyo near Guerrero, Baja California.

RESULTS

Just as Hunter & Brown (1965) showed in *Chaetopleura* and *Lepidochitona,* there is an asymmetry of the right and left sides in the chitons studied. It is evident when one compares the average number of gills per side with the length of an animal, that the right and left sides are not similar. Growth seems to be random. This is easily seen by comparing the gill numbers on either side of *Tonicella lineata* in Figures 1 and 2. Thus, it appears that Hunter & Brown's work is correct.

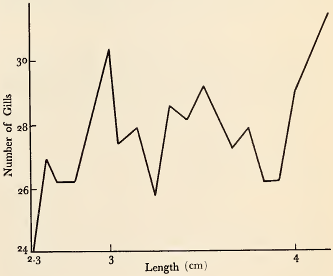

Figure 1

Graph showing the number of gills found on the right side of *Tonicella lineata* of different lengths.

But much more is evident from my data, as may be seen in Figure 3. Those chitons which eventually reach a "large" adult size (8 to 9 cm) have more gills than do those which attain only a "small" adult size (1 to 5 cm). The difference is quite obvious when one compares animals of the same sizes, between 0.5 and 5.0 cm, but of different adult sizes. Thus, some may have adult stages larger than 5 cm and some may not. The "large" chitons are from at least 2 species and 2 different families, yet

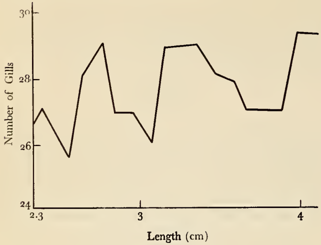

Figure 2

Graph showing the number of gills on the left side of *Tonicella lineata*. A comparison with Figure 1 demonstrates the lack of symmetry between the two sides.

they possess on the average from 4 to 10 more gills per side than do the "small" chitons (which include even representatives of 2 different suborders). Thus, there is some major difference between "large" and "small" chiton growth.

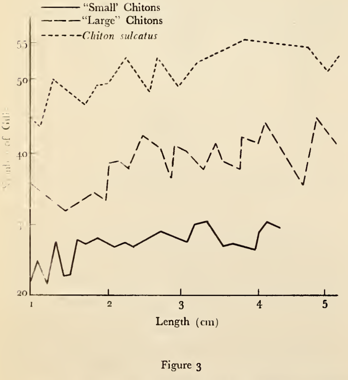

Figure 3

[illegible] chitons have more gills than "small" chitons at all lengths

Chitons of different adult size have the same effective gill surface per unit length. This is found by comparing the gill cavity area with the length as in Figure 4.

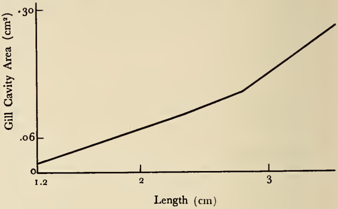

Figure 4

Both "large" and "small" chitons have equal gill surface area per unit length

The difference between "large" and "small' chitons is found when one compares the gill series lengths with the body lengths, and the length of the last gill with the length of the gill series. It appears that the length of the gill series of the "large" chitons are somewhat longer than in the "small' chitons, even when both groups are of the same lengths (Figure 5). And the "small" chitons

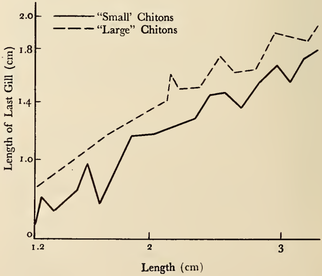

Figure 5

"Large" chitons have longer gill series than "small" chitons achieve equal gill cavity area by lengthening their gills more than the "large" chitons do (Figure 6). Thus, the most posterior gill of the "small" chitons are longer than the last gill of "large" chitons of equal length. In other words, the "small" chitons have shorter, wider gill cavities than do the "large" chitons.

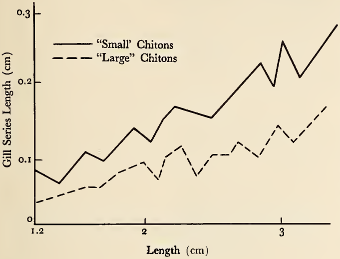

Figure 6

"Small" chitons have longer gills than "large" chitons

DISCUSSION

Hunter & Brown (1965) may be correct regarding the non-segmented nature of an "ancestral mollusk" type. In fact, my results seem only to support that part of their arguments. The right and left gills of chitons are never completely equal in number.

Deciding that the "ancestral mollusk" was not segmented does not necessarily support Yonge's hypothesis of a two-gilled ancestor. The additional information I have supplied about the chiton gill cavity adds a new perspective to the problem. If the many gills in chitons are due to a forced multiplication of them due to the chitons' being flattened over evolutionary history, why do "large" and "small" chitons differ? If each type, "large" and "small", was achieved separately, why do such similar animals, as those found in the same family, have differently shaped gill cavities? Thus, it seems that Yonge's hypothesis fails to account for these differences in gill cavity shapes.

A simple and more adequate explanation would be that the multiplicity of gills as seen in *Neopilina* or the chitons may be like the primitive condition of the molluscan gills. It seems much more plausible that the two trends seen in the "large" and "small" chiton gill cavities were present in the "ancestral mollusk" and have been maintained by the chitons, than that they were the result of a couple of stages of flattening of the animals. Thus, the two gills found in gastropods and lamellibranchs and the four gills in some cephalopods are most probably the product of a reduction in number of gills with an enlargement of the posterior part of the gill cavity. This reduction in the number of gills would, of course, obliterate the pattern of "small" and "large" animal gill areas. Therefore, it appears that the chitons have maintained a condition found in the "ancestral mollusk" type, although more gills may have been added, since the chitons have so many more gills than does the more primitive *Neopilina.*

SUMMARY

Chitons of "large" adult size have more gills present on both sides of the animal at all sizes than do the "small" adult-size chitons. The difference in number does not affect the effective gill surface per unit length. The effects of the difference in number on the area of gills are equalized in the "small" chitons by possession of longer gills. Therefore, the "large" chitons have long narrow gill cavities, while the "small' chitons have short wide gill cavities.

These two trends in the chitons do not seem to be adequately explained by Yonge's hypothesis as to the origin of the multiplicity of gills in chitons. A more adequate explanation is that the trends were present in some "ancestral mollusk" type and have been maintained in the chitons and in *Neopilina.* All other mollusks have, therefore, modified this primitive gill cavity.

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